

Vol. 113. Pt. 5. Pp. 101-121. 2 Plates. 11 figs. 11th July, 1961

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LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

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2 plates.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 10s. 0d.

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DEFENSIVE ODOURS AND MULLERIAN MIMICRY AMONG INSECTS¹

By MIRIAM ROTHSCHILD

Manuscript received 13th September, 1960

(Read 7th December, 1960)

(With 1 Plate and 11 Text-figures)

INSECTS have many and varied predators to contend with. In the past attention has been centred chiefly on the adaptations developed to protect them from attack by birds. This is due to the fact that both entomologists and birds hunt by sight. Only relatively little attention (Cott, 1940) has been paid to odour and sound production developed to protect them from colour-blind predators which hunt largely by the sense of smell, hearing or vibration.

Collectors have recognised two main types of insect odours :

- (1) those which are produced when the animal is disturbed or threatened, and are assumed to have a repellent or warning (defensive) function ;
- (2) those which are not produced as a reaction to a threatening situation and are assumed to function as recognition signals (frequently carried for long distances) between members of the same species, or alluring, attractant and stimulating scents operating between the sexes, especially during courtship.

Collectors do not seem to have been impressed by the fact that a number of these warning smells resemble each other. It seems to me probable that we are here dealing with an aspect of Müllerian mimicry, and that there exists a widely distributed complex of rather similar scent patterns which function as warning mechanisms for colour-blind predators, in the same manner as red and yellow, yellow and black rings, and the other well known aposematic patterns function as warning signals for predators which hunt by sight.

It is, of course, much more difficult for the human observer to compare a series of scent patterns than to compare a series of colour patterns. The sense of smell is rather poorly developed in man and often impaired by personal habits such as smoking, and furthermore smells cannot be compared simultaneously side by side like a series of colours. Until now they have had to be memorised and then compared in a sequence. Nor do they lend themselves easily to accurate verbal description and are often extremely complex. However, the ability to perceive and compare subtle shades of difference in aroma and flavour can be developed with practice, a fact well known to all professional wine, tea and butter² tasters.

¹ An abridged version of this paper was read at the XIth International Congress of Entomology, Vienna, August 1960.

² McDowall (*Buttermakers' Manual*, 1953) states that there are six fundamental odours in butter and that all the innumerable variations are combinations of these. The attractive flavour is due to diacetyl



In strong solutions it is coarse and unattractive, but in dilute form in butter it contributes fragrance and fullness of flavour. This author lists fifteen flavour defects in fresh butter and twenty further flavour defects developing after manufacture.

An insect smell which has attracted some attention in the past is that of the yellow defensive secretions of Ladybirds (Coccinellidae), and this is probably one of the fundamental ingredients of this particular type of warning scent pattern. To the human nose this scent appears to be a quinolene derivative, perhaps isobutyl quinolene or something which smells the same. In the literature there are many scattered references to this scent occurring in unrelated aposematic insects. The defensive secretion (Pl. I, fig. 1) from the prothoracic (cervical) glands of the Garden Tiger Moth (*Arctia caja* (L.)) has been reported to smell of Coccinellids by Zeller (1840), Portschinsky (1892), Dinger (1922), Zerny & Beir (1936) and Lane (1956). The butterflies *Amauris echeria* (Stoll), *Alaena amazoula* Boisduval and *Acraea horta* L., all well known distasteful species, are also reported to exude a yellow fluid from the thorax and wing veins which smells like Coccinellids (Marshall, 1902; Swynnerton, 1915; Poulton, 1890). Various beetles such as the fulvous and black *Clythra wahlbergi* Lacordaire and the black and red Braconids, *Bracon coccineus* Brullé, *Iphiaulax pictus* Brullé and *I. flagrator* Gerstaecker are all said to smell strongly like Coccinellids. The supposition that this "Ladybird" or quinolene-like smell is an important element in a main warning scent pattern occurred to me when I was collecting in the field and realised that an assembly of aposematic insects present, which included three separate Orders: Burnets (*Zygana*) and the Cinnabar Moth (*Hypocrita jacobaeae* (L.)), Ladybirds and the Soldier Beetle (*Rhagonycha fulva* (Scopoli)) and the Froghopper (*Cercopis vulnerata* Germar), all possessed this peculiar and particular odour. The same smell has been noted by Lane & Rothschild (1959) in the Cardinal Beetle (*Pyrochroa serraticornis* Scopoli), Ruby Tiger (*Phragmatobia fuliginosa* (L.)), Cream Spot Tiger (*Arctia villica* (L.)), Scarlet Tiger (*Panaxia dominula* (L.)) (Pl. I, fig. 2) and Black Arches Moth (*Lymantria monacha* (L.)). I have since identified it in both Ermines (*Spilosoma lutea* (Hufnagel) and *S. lubricipeda* (L.)), the male Muslin Moth (*Cyenia mendica* (Clerck)), the Forester (*Procris* sp.), Jersey Tiger (*Euplaguea quadripunctaria* (Poda)) and several Footman Moths (Lithosiinae) and *Rhyparia purpurata* L.

The smells of the defensive fluid secreted by these species have several other features in common. If inhaled they produce a disagreeable "gassy" sensation in the nostrils and in the back of the throat, which is generally associated with very volatile substances such as ammonia or petrol, and comes close to physical pain or discomfort. Children especially complain of a sore feeling inside the nose. Observers attempting to describe this element choose such words as "gaseous", "pungent", "acid", "penetrating", and so forth, but none of these terms is satisfactory. Among moths this feature of the smell is most pronounced in the Burnets (*Zygana*) and Jersey Tiger (*E. quadripunctaria*), and in my own case inhalation is followed quickly by an attack of asthma. Another feature common to all these species is a plantlike scent which mingles with the Ladybird or quinolene-like odour. This smell has a quality reminiscent of various essential oils, but it is extraordinarily elusive in nature. The different species have markedly different scents, yet again and again observers liken them to the same series of plant scents. Thus they have frequently been described as smelling of verbena, the juice of poppy stalks, the leaves of tomatoes, ragwort, crushed pea-pods, legumes, thyme, mint, pine needles, hedge-garlic, red currant leaves etc. Zeller (1840), for instance, described the defensive gland secretion of the Garden Tiger (*A. caja*) as "smelling of Coccinellids or the juice from the stalks of poppies", while Swynnerton (1915) describes the protective juices of one species of *Acraea* as "smelling strongly of the bitter juice of poppy stalks", and a related species of *Acraea* as "smelling strongly of Coccinellids". Several observers, however, have agreed that the plantlike element in the smell of the defensive glands of *A. caja* is similar to that of the stinging nettle (Uffeln, 1909; Zerny & Beier, 1936; Lane, 1957) and with this I am in agreement. I am also of the opinion that the smell of the secretion of Ladybirds includes this nettle-like odour. This is much more obvious in *Coccinella 11-punctata* L. than in either *C. septem-punctata* L. or *Adalia bi-punctata* (L.).

Sometimes in *11-punctata* the stinging-nettle element is so strong³ that it virtually swamps the more familiar Ladybird scent. If one passes the filter paper impregnated with this secretion through a stream of liquid air, and then heats the container in an oil bath, the quinolene-like smell disappears and one is left with a more or less pure nettle odour.

Despite the great variety and subtle variations in the smell of these defensive glands, which suggests the presence of a large number of different elements,⁴ one nevertheless also gets the impression that there is a general character to this particular defensive scent pattern which is dependent on the presence of a few basic ingredients. Among these are probably terpenes or substances which smell like them to the human observer.

This is supported by the fact that quite a high proportion of adult individuals (Schulze, 1913; Lane, 1956) cannot detect any odour whatsoever from the exudate from the glands of *A. caja* or *P. fuliginosa*. Do these "non-perceivers", who constitute about 10 per cent. of the people tested, indicate a polymorphism in man (similar in character to those who fail to taste phenylthiourea or to smell Freesias) or is this a rather subtle threshold effect dependent on the age and habits of the individual, especially marked in those who work, for example, in chemical laboratories⁵ and are constantly exposed to strong smelling substances in heavy concentrations? Many people tested fail to detect the characteristic smell of the stinging-nettle if the plant is in the sun, but spraying with water enables them to perceive the odour. Others, again, can only apparently smell the plant if the leaves and stem are crushed. Marshall (1902) could taste the juices of *Acraea horta*, which he described as bitter,⁶ but, unlike Trimen (1897), he was unable to detect any smell at all in this species.

Many, but not all, the scents of this particular pattern have the additional and clearly useful quality of persistence (Trimen, 1897). The secretion from the glands in the legs of the Ladybird is oily, which no doubt enhances this quality. In the case of

³ Children possess a noticeably keener sense of smell than adults. A piece of filter paper with a minute drop of Ladybird (*C. 7-punctata*) secretion placed upon it was handed to Miss Ann Benson, aged nine. Asked what the paper smelled of, she replied instantly "Nettles". Five adults present were unable to detect any smell whatsoever.

⁴ A professional scent tester, on sniffing the exudate from *A. caja*, made the following comment: "This scent is very complex. The top note is acrid, reminiscent of, for example, caryophyllene. Initially could contain C_{10} terpenes, e.g. pinene, but these do not seem responsible for the main odour. This might be partly due to a material such as borneol. Unsaturated C_6 , C_8 and C_{10} alcohols also give "leafy" effects of this type, with suggestions of "fatty" which are also present. Such compounds as fenchyl alcohol, fenchone. The deeper leafy note is simulated by certain alkyl-aryl acetals and ethers, such as cyclic acetals of β -phenylacetaldehyde with glycols and alkyl ethers of β -phenylethanol. Some of these compounds also have the fungal type of odour which becomes more apparent with time, as some components fade owing to evaporation. The "vegetable" odour is also simulated by certain gum resins—e.g. elemi resin—which contain mainly terpenes and sesquiterpenes."

⁵ It is interesting that one worker in the Inorganic Chemistry Laboratory (Oxford) was quite unable to smell the British races of *A. caja* but had no difficulty in perceiving quite a strong odour in a race from northern France (Reux, Calvados), the smell of which he likened to cats. It will be recalled that one observer also likened—most emphatically—the smell of the exudate from the gland of *P. fuliginosa* to cats (Lane, 1956). It is possible, therefore, that there is geographical variation in scents as well as other morphological characters and that with the perfection of the technique of gas chromatography this character will become one of the recognised criteria for distinguishing geographical races. However, nothing is at present known of the extent of variation of odours within a species and it is quite possible that odour variation is as usual in *A. caja* as wing pattern variation.

⁶ The author finds that *A. insignis* Distant gives off a vapour which affects the eyes in much the same manner as the vapour from menthol crystals dissolved in water. Inhalation by some subjects is followed by quite a severe headache.

several moths, particularly the Arctiids and Hypsids, the haemolymph⁷ is mixed with the secretion of the defensive gland, which gives it a cloying, somewhat oily consistency. The fluid from the glands of fresh specimens of the Ruby Tiger (*Phragmatobia fuliginosa*), when expressed on to a glass slide, thickens and sticks to the surface, retaining its odour for twenty-four hours. On the other hand, the scent-producing fluid of the Burnets (*Zygaena*) and Foresters (*Procris*) is not oily, nor is it mixed with haemolymph,⁸ and it is extremely volatile; when a drop is placed on a slide, it evaporates quickly, leaving no trace on the glass. It should be remembered that some form of oil or grease is almost invariably added to commercial preparations of scent to increase their "lasting quality".

Gas chromatography⁹ has placed a new tool at our disposal. When this technique is developed and adapted for the purpose it should be possible to produce chromatograms (see figs. 1-9) of the secretions of the defensive glands of moths and other insects, and it will then be possible to compare the scent patterns side by side instead of relying on a difficult and uncertain form of memorisation. An investigation of an extremely preliminary nature has shown that the defensive glands of several species of insects produce chromatograms which have certain features in common. The preliminary nature of these investigations must be emphasized since it has not yet been possible to identify the chemical constituents dealt with. The columns were not constructed to record the presence, for instance, of quinolene.

In all these chromatograms, groups of early "peaks" can be observed (figs. 1, 3, 4, 6, 8, 9), which indicate the presence of highly volatile substances with low boiling points and a small number of carbon atoms. Such early "peaks" are absent¹⁰ in chromatograms of the Cabbage White butterfly (*Pieris napi* (L.)) and the large Yellow Underwing moth (*Triphaena promuba* (L.)) (fig. 2), species which have no defensive glands of this particular type. When unrelated species (fig. 3) are being dealt with, the position of individual "peaks" suggests that these represent different substances and that we are dealing with a similar and general effect (including actual odour) arrived at by a combination of different chemicals. It is perhaps unnecessary to point out that there are many different substances which are claimed to smell alike to the human nose (see Moncrieff, 1951, *The Chemical Senses*, Chap. 9), such as benzaldehyde, an aromatic aldehyde with a boiling point of 179.5° C., and the gas,

⁷ This has been recorded by Windecker (1939) for *H. jacobaeae*, and for a Hypsid, *Caryatis syntomina* Butler, by Grassé (1941). I have confirmed the presence of blood cells in spontaneous emissions (i.e., without handling or pressure) from the defensive glands of *A. caja*, *H. jacobaeae*, *P. dominula* and *E. quadripunctaria*. The number of blood cells in the exudate varies from species to species. They are relatively very dense in *H. jacobaeae*. Also there are fewer blood cells in the first few drops secreted by *A. caja*—the haemolymph seems to be a secondary feature of the emission.

⁸ If the insect is nipped by a predator, the haemolymph squirts out from specialised areas on the thorax and then almost certainly becomes mixed with the scent-producing fluid on the anterior part of the moth's body. The same effect would thus be achieved by a somewhat different method. The haemolymph itself is odourless to the human observer.

⁹ The gas chromatography was carried out in Dr. Courtenay Phillips' Laboratory, Inorganic Chemistry Department, Oxford University, by Dr. P. Cartoni, Mr. Robert Lowry and Mr. John Shore. A one metre column consisting of celite coated with silicone oil, dinonyl phthalate or Apiezon "L" was used. The carrier gas was nitrogen and the detector a hydrogen flame ionization.

A trap consisting of a 500 ml. flask was used, whereby all the volatile material from living insects could be collected and passed onto the column. Another method was devised whereby the secretion from different glands could be collected on filter paper, placed directly in the U-tube shown in figure 11 and from thence passed into the column.

¹⁰ The nature of the single very large peak in fig. 2 is not clearly understood. It may be in some way connected with the death of an insect in the flask.

hydrogen cyanide, with a boiling point of 26°C . Related species, however, such as the 7-spot and 2-spot Ladybirds (*Coccinella septem-punctata* and *Adalia bi-punctata*) have chromatograms with certain features in common (fig. 4) and to the human nose appear identical in quality of scent, though not in intensity.

In the nettle (*Urtica dioica* L.) (fig. 3) methyl alcohol (methanol CH_3OH) and pinene have been identified. In the Garden Tiger (*Arctia caya*) a similar "peak" has also been identified in the same region (fig. 6), which may be methanol, but pinene appears to be absent.

However, in the chromatograms of both the Garden Tiger and the Ladybirds there is a peak (fig. 1 (g)) in the essential oil region. It must, of course, be understood that the substances are being dealt with in minute quantity, of the order of $0.01\text{ }\mu\text{gm}$. There might, consequently, also be minute quantities of pinene present, which were not detected in the column.

A remarkable similarity, which can be designated as convergent evolution of scent patterns, is found between the chromatograms of two moths which are in no way related yet have a very similar aposematic colour scheme and defensive scent: the Burnet (*Zygaena lonicerae* (von Scheven.)) and the Scarlet Tiger (*Panaxia dominula*) (fig. 7). In this case a less sensitive column was used and the whole moth, not merely the gland exudate, was put into the trap and its volatile products passed on to the column. Moths have numerous glandular secretions, not all of which are defensive in character, and some of these may have been recorded as well.

As I have said earlier, in many species a variable quantity of haemolymph is pumped out of the same aperture as the repellent fluid of the prothoracic (cervical) gland. A chromatogram was therefore attempted of the haemolymph of *A. caya* (fig. 6 (4)), drawn directly from the abdomen and thorax, and this shows the presence of only one large single peak, which probably corresponds with the peak (e) present in the gland secretion (figs. 6, 6a, (e)).

There is also a peak, apparently absent in the secretion of the exudate of the cervical glands from females, which is present in males (fig. 6a (b)). Owing to the fact that there is considerable variation in the amount of haemolymph and scent material present in the exudate of moths from different broods, it would be unwise to do more than draw attention to this detail in the chromatogram in question. One of the three chromatograms in this figure is made from meconium obtained from the caecal sac. A very early "peak" occurs here (fig. 6a), which is also obvious on chromatograms of the whole moth. I myself have long subscribed to the theory that the meconium is involved in a defensive mechanism. Some meconium, such as that of *Papilio machaon* L., has a very strong scent, and in many characteristics is reminiscent of the exudate from the defensive (cervical) glands of *A. caya*. For instance, when inhaled it also gives me a certain type of asthma.

FUNCTION OF THE ODOUR

It has often been suggested, and also assumed, that the smell itself, probably associated with a bitter taste (which, for instance, is characteristic of quinolene) is the disagreeable attribute of the aposematic insect. The fact that, to the human nose, this scent is not particularly nauseous, and in fact often agreeable, is no reason for assuming its effect on animal predators is similar. Many smells which are to us particularly revolting are unquestionably alluring to other mammalian species, and the reverse situation may well occur. However, scattered throughout the literature are numerous references to feeding experiments in which animals have eaten several specimens of an aposematic insect in quick succession, obviously unaffected and undeterred by either smell or taste (Poulton, 1887; Beddard, 1892; Marshall, 1902) but soon afterwards they regurgitated the insects and subsequently persistently refused the species as an article of diet. In other cases there have been no noticeable

after-effects, but the insect in question has been subsequently rejected on sight, possibly also on scent. This type of behaviour has been observed in mammals, birds, lizards, frogs, toads, spiders and mantids. I have confirmed the last type of reaction in the case of the Himalayan Crested Tit (*Macholophus xanthogenys*), and Terrapins with *H. jacobaeae* and the House Mouse (*Mus musculus*), with *P. dominula* and *Abraxas grossulariata* (L.).

My own belief is that these aposematic insects contain a poisonous or unwholesome element which causes discomfort, nausea or pain *after* they have been swallowed, and that both the bright colour pattern and scent pattern are part of a mechanism which directs the attention of different types of predators to these dangerous qualities. This was suggested many years ago by Marshall (1902) and Swynnerton (1915). The former wrote "mere unpleasantness of taste would be hardly sufficient to give so great an immunity from attack . . . as is apparently enjoyed by the Danainae and Acraeinae unless accompanied by poisonous or unwholesome qualities". Swynnerton was more emphatic and stated categorically: "Indigestibility is the real defence".

Mühlmann (1934) also showed that his experimental birds were indifferent or soon became accustomed to such strong tasting substances as clove oil, mustard, quinine and sulphate of magnesia, but that tartar emetic, which acted upon the crop and stomach besides, presumably, the sense of taste, had a more lasting deterrent effect.

The work of Southern and his collaborators (Chitty and Southern, 1954) has demonstrated how quickly rats and mice become bait-shy after ingesting non-fatal doses of poisons. It is assumed that the smell and flavour of the base (rolled oats, sugar rusk, etc.) are the elements they identify and subsequently associate with the poison. A change of base will often result in fresh kills.¹¹

No experiments that I am aware of have been carried out to test whether or not birds detect the odour of the defensive glands. The secretions of most of these glands which have been tasted by man, such as those of Coccinellids, Acraeines, Arctiids, Hypsids, etc., are reported to have, for the human palate, a slightly bitter or acid taste (Ford, 1955; Grassé, 1941; Zeller, 1840; Griffiths, 1890; Marshall, 1902; Trimen, 1897). It has been demonstrated that in the case of *A. caja* (Bissett, Frazer, Rothschild & Schachter, 1959) this substance, in addition to the scent producing substance, contains a choline ester ($\beta\beta$ -dimethylacrylylcholine) which is capable of damaging animal tissues. It is, therefore, probably a question of taste, combined with odour and possibly a burning sensation, which causes the hasty rejection of many aposematic insects when first seized either in the beak in the case of birds (Griffiths, 1890; Marshall, 1902; Swynnerton, 1915; Windecker, 1939; Brower, 1958) or when mouthed (Carpenter, 1921; Pitman, 1929) by monkeys and lemurs. There is one record of a tame robin which definitely recoiled from fingers contaminated with the secretion of the defensive glands of *A. caja* or Ladybirds (Dingler, 1922). In my own experiments bush babies (*Galago*) and mice have been observed to shrink back hastily from filter paper impregnated with the defensive gland fluid from Arctiids and Ladybirds and also from filter paper contaminated by the body fluids of wasps (*Vespula germanica* (Fab.)). In the latter case these papers seemed to me to be completely scentless, but wasps are distasteful to most birds (Mostler, 1935; Lane, 1957) and many insectivorous mammals, quite apart from the question of their stings, and it is not surprising to find that they have a disagreeable smell even though the human nose is too insensitive to detect it.

It may be a mere coincidence, and without significance, that the smell of the stinging-nettle (*Urtica dioica*) resembles that of distasteful insects such as *A. caja* and the Ladybirds. It is also possible that the same warning mechanism has been

¹¹ My own experiments have shown that hens fed upon grain coated with Panogen and Aztex (a Shell insecticide) will come to associate unpleasant after-effects with the grain about a fortnight after the initial feed and thereafter refuse it. It is not yet understood by which sense they distinguish between treated and untreated grain.

developed by the plant, which is thus included in the whole Müllerian complex. There is certainly no doubt that many herbivorous mammals avoid the stinging-nettle, especially if other green plants are available, although in hard weather horses will sometimes eat them just as Tits (Betts, 1955) and Green Tree Frogs (Poulton, 1890) will eat Ladybirds in the winter.

The essence of warning colour patterns or scent patterns pertaining to the Müllerian type of mimicry (Poulton, 1890; Carpenter, 1921; Jordan in Morton Jones, 1932; Morton Jones, 1934) is that the immunity conferred is relative and not absolute. It is not, of course, suggested that the nauseous, toxic or poisonous element in all aposematic insects is similar. In fact, the reverse is almost certainly true. For instance, certain toxic or irritant substances found in the abdominal tissues of *A. caja* (Bissett, Frazer, Rothschild & Schachter, 1959) are not present in the related species, *P. fuliginosa* (Frazer & Rothschild, *in preparation*), and histamine, which has been demonstrated in relatively heavy concentrations in the White Ermine (*S. lubricipeda*), is totally absent in the Buff Ermine (*S. lutea*). As already emphasized, it is not suggested that the similar odours of the defensive glands are all produced by the same substances; in the same way the warning red pigments of insects are not all chemically similar (Ford, 1941, 1942, 1944a,b, 1947), although they frequently perform a similar function.

There may be some insects, like some plants, which are so poisonous that no predator will accept them under any circumstances. There are others which are rejected by a certain proportion of insect eaters but accepted by others,¹² and again there are predators which, like the cuckoos and the hedgehog, are specialized feeders adapted to a diet of generally distasteful and unwholesome species.¹³ But, broadly speaking, aposematic insects (other than the Batesian mimics) are sufficiently unpleasant as food to enable them to adopt a risky form of advertisement, using easily recognized characters by which they attract attention in order to divert it. It is thought that in this sense certain scent patterns are a complementary attribute to warning markings in "unpalatable" insects and that Müllerian mimicry applies to smell as well as to colour and pattern.

It seems extremely likely that a more careful investigation will reveal true Batesian mimics among the Lepidoptera which have developed similar scent as well as similar colour patterns to their models.

ACKNOWLEDGMENTS

I wish to record my gratitude to Dr. Courtenay Phillips and the research students in his department for the generous sacrifice of their time and the infinite trouble they have taken with the gas chromatography and the solution of the various problems involved. It would be impossible for me to mention all those who have kindly provided me with material, but I would especially like to thank Mr. R. H. Carcasson for sending me living *Acræa insignis* from Nairobi, and Charles and Charlotte Lane for collecting many hundreds of ladybirds. I would also like to record my gratitude to Eric Remington for the capturing of four Great Tits, and to Rosie and Josie Lane for rearing and caring for Short-tailed Field Voles, Long-eared Bats, Bushbabies and many other caged predators.

¹² It must not be forgotten that a repulsive odour may protect an insect which is unacceptable to mammalian or arthropod predators, but, to escape attack by bird predators which are unaffected by the indigestible qualities and the smell in question, the same insect will resort to crypsis. Such an explanation could account for the cryptic colour of certain Pentatomid bugs, which are eagerly eaten by many birds (Marshall, 1902) but rejected by mammals, such as the coati (Myers, 1930), an animal with deficient eyesight which hunts principally by the sense of smell.

¹³ The Loggerhead turtle eats the Portuguese Man o' War. This is an extreme example of this type (Wangersky & Lane, 1960). The hen is also said to be resistant to cantharidin (Kaiser & Michl, 1958).

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POST-SCRIPT

An interesting paper appeared recently, "The biology and behaviour of *Poecilocerus bufonius* Klug, with special reference to the repellent gland (Orth. Acrididae)" by L. Fishelson (1960, *Eos, Madr.* **36** : 41-62) which has bearing on several points raised here. The author shows that :—

(a) the secretion of the defensive glands of *P. bufonius* is poisonous and has a pungent odour.

(b) the haemolymph of *P. bufonius* is also poisonous.

(c) mice with previous experience of *P. bufonius* run away from the smell of the defensive glands—for example, if a tube contaminated with the fluid is introduced into the vicinity of the mouse.

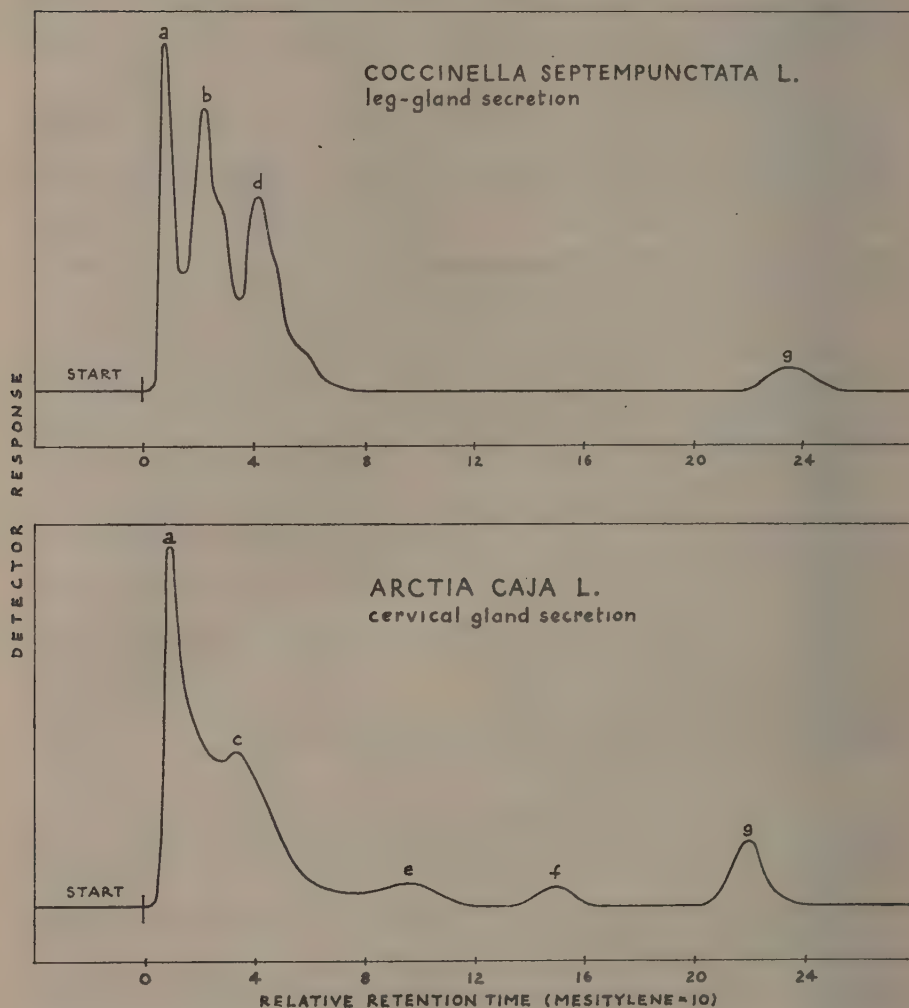


FIG. 1.—Comparison of the chromatograms of the Garden Tiger (*Arctia caja* (L.)) and the 7-spot Ladybird (*Coccinella septempunctata* L.).

All peaks marked with the same letters are considered to represent identical substances. Peak *g* lies in the "essential oil" range.

Column: Apiezon "L." Temperature: 156° C.

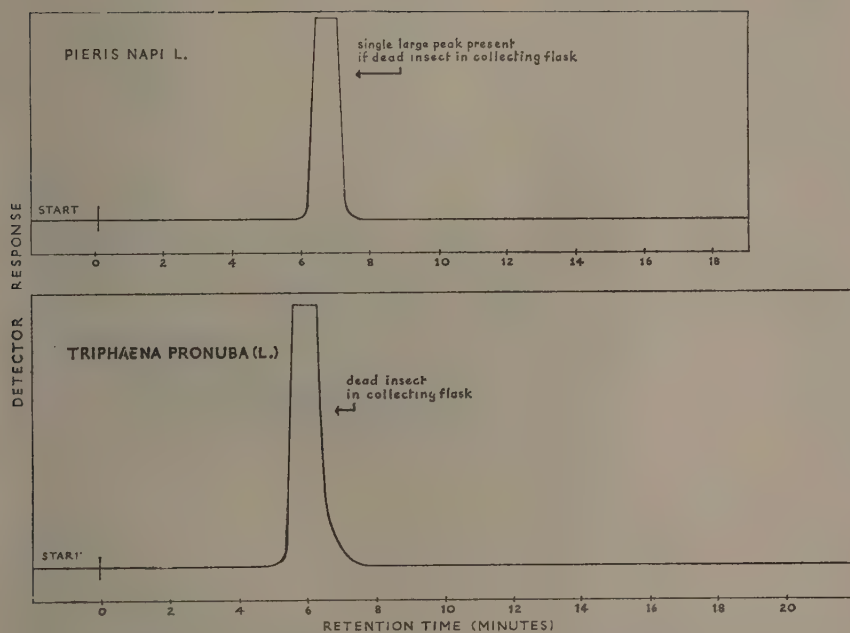


FIG. 2.—Chromatogram of vapour from whole insects of Small White Butterfly (*Pieris napi* (L.)) and Large Yellow Underwing (*Triphaena pronuba* (L.)).

Note the large single peak always present if an insect died while in the collecting flask, and the absence of early peaks.

Column: Apiezon "L". Temperature: 66° C.

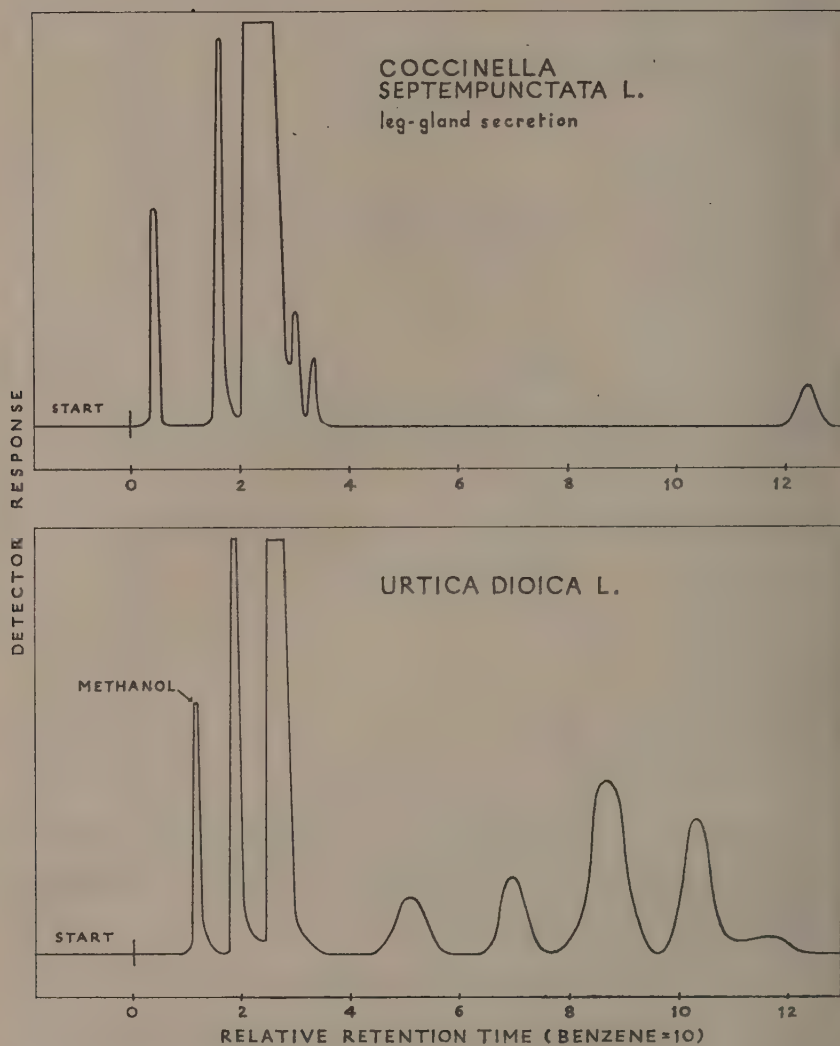


FIG. 3.—Chromatogram of the 7-spot Ladybird (*Coccinella septempunctata*) compared with that of the Nettle (*Urtica dioica* L.).

There are many dissimilar substances in the low boiling range.

Column: Silicone oil 707. Temperature: 20° C.

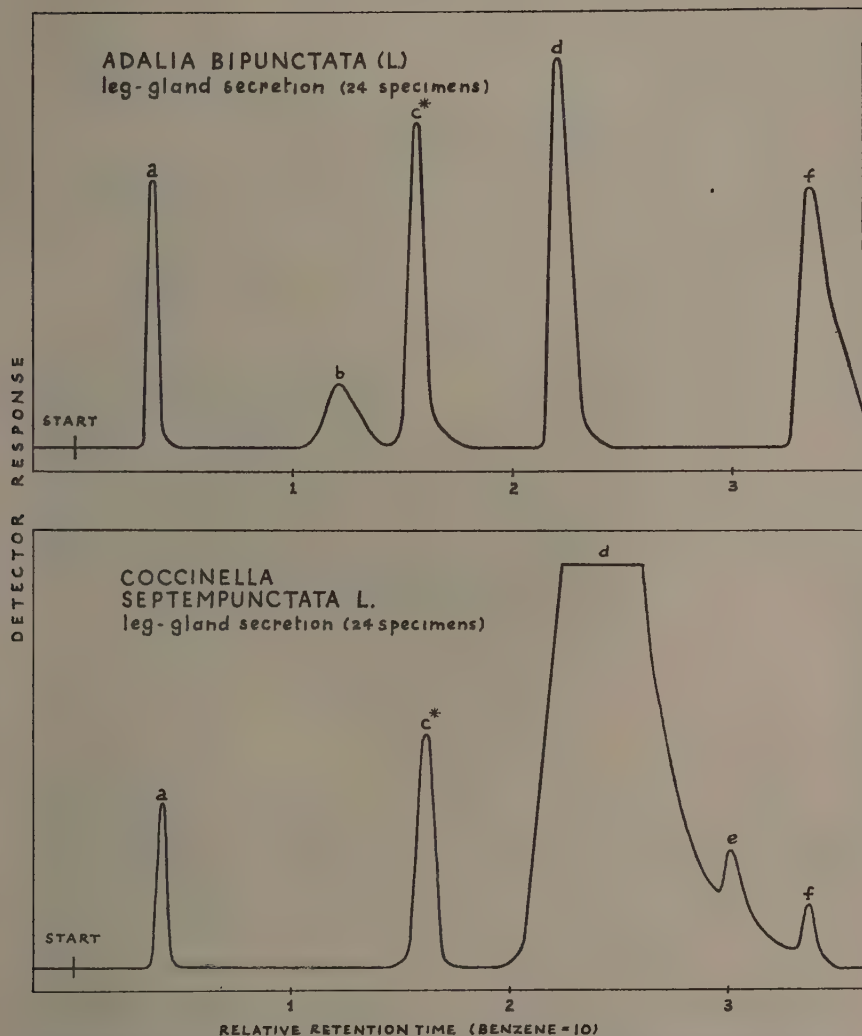


FIG. 4.—Chromatograms of two species of Ladybird (*Coccinella septempunctata* and *Adalia bipunctata*), showing that similar substances are present in both although the relative amounts differ.

Peak *d* is too large to show in its entirety and has therefore been cut on the figure. This procedure is adopted in all the diagrams.

Column: Silicone oil 707. Temperature: 20° C.

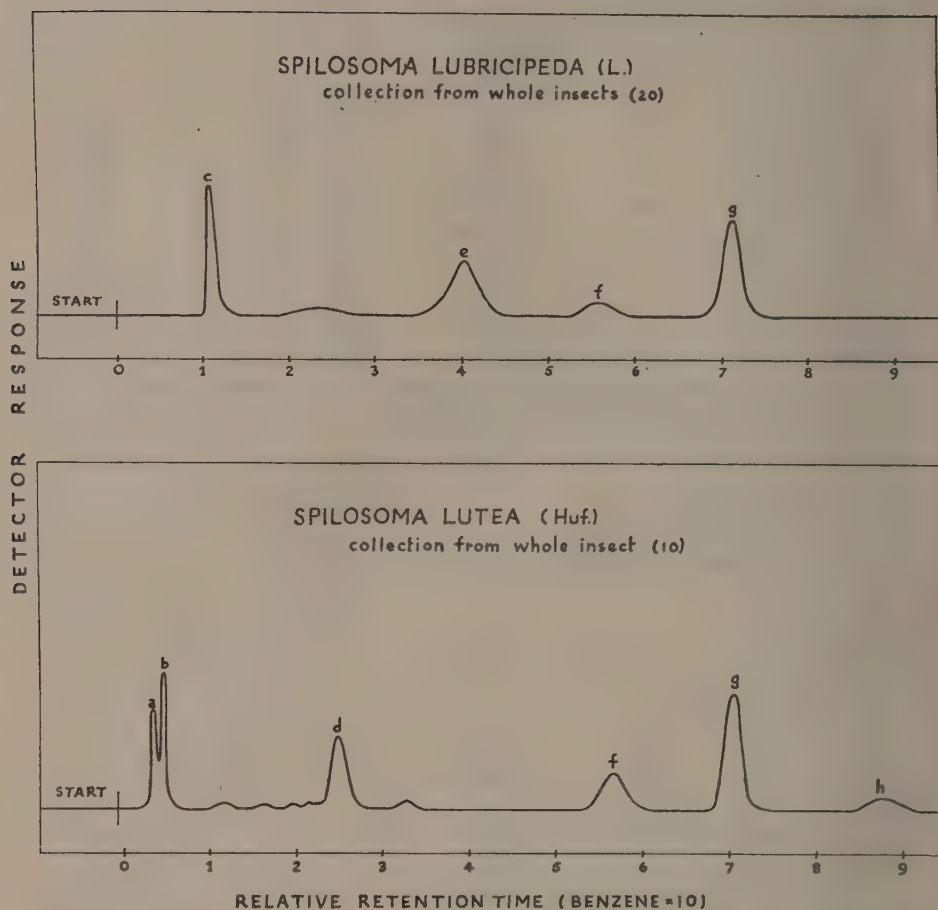


FIG. 5.—Chromatograms of White and Buff Ermines (*Spilosoma lubricipeda* (L.) and *S. lutea* (Huf.)). Collection from whole insect.

These two chromatograms were expected to resemble each other more closely since the odours of the defensive glands are similar in kind though not in intensity. The Buff Ermine, which smells less strongly, is more acceptable to predators than the White Ermine.

Column: Dinonyl phthalate. Temperature: 20° C.

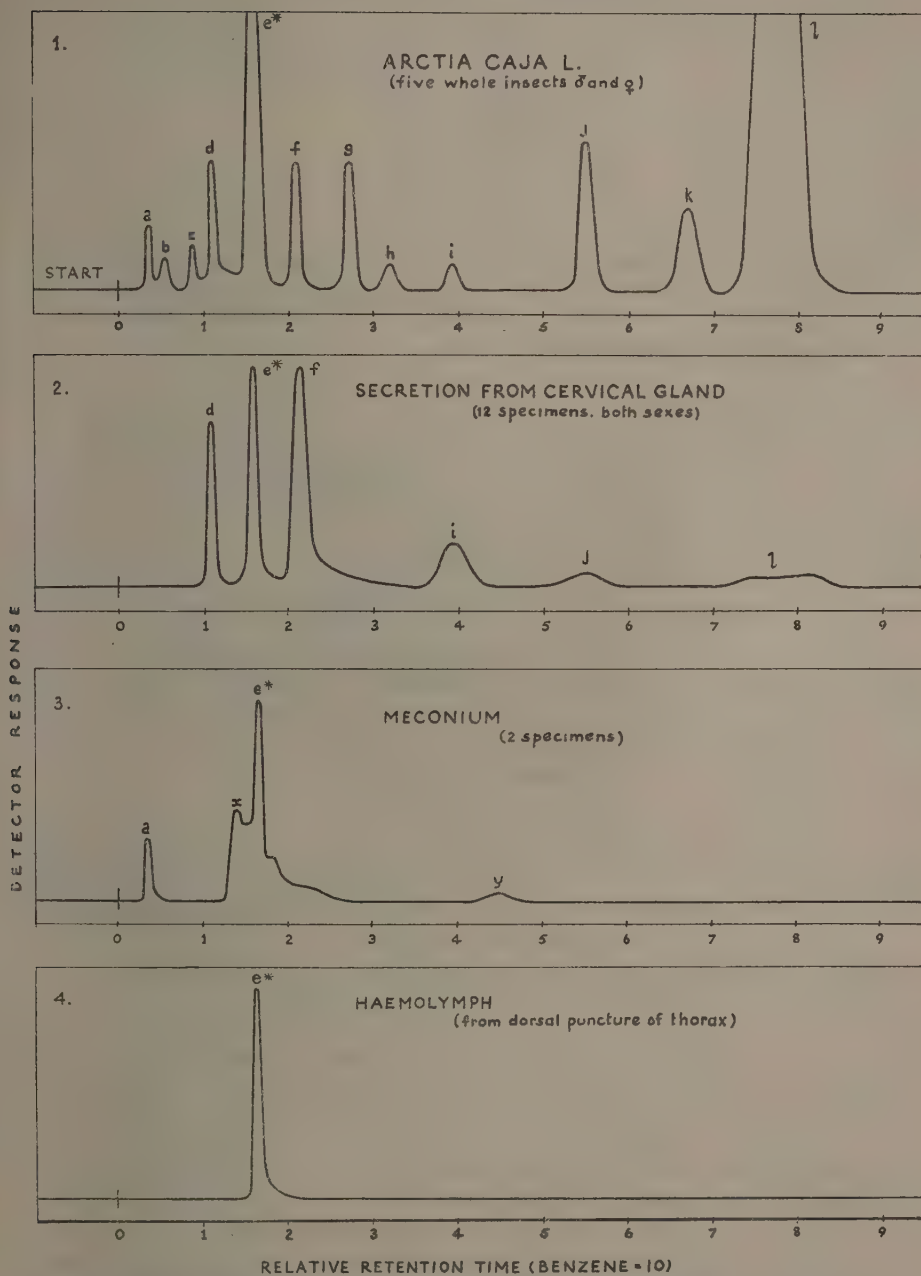


FIG. 6.—Chromatogram of *Arctia caja* L. (1) Collection from whole insect; (2) secretion of cervical gland; (3) meconium; (4) haemolymph.

Only peak e* is present on all four chromatograms. Peaks x and y are peculiar to the chromatogram of meconium.

Column: Silicone oil 707. Temperature: 20° C.

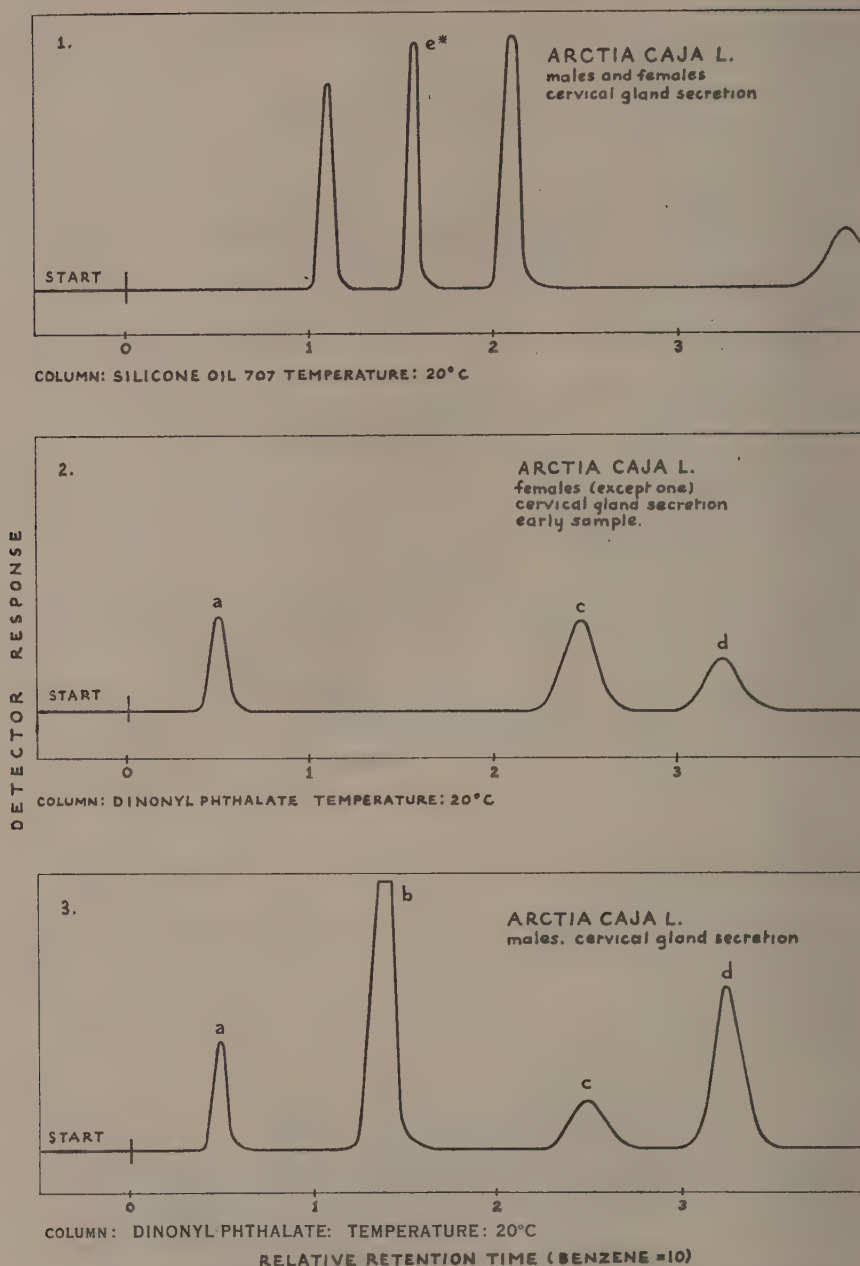


FIG. 6a.—Chromatograms comparing cervical gland secretion from males and females of *Arctia caja* L.

Note the amount of haemolymph present in the gland secretion varies enormously from moth to moth and even from right to left side of an individual moth. In those moths which supplied the secretion for (3) the exudate was colourless; apparently little, if any, haemolymph being present.

The chromatograms have been idealized to make the point clear.

The large peak *b* (3) indicates the presence of some substance in the cervical gland secretion of males, which is absent in that of the females.

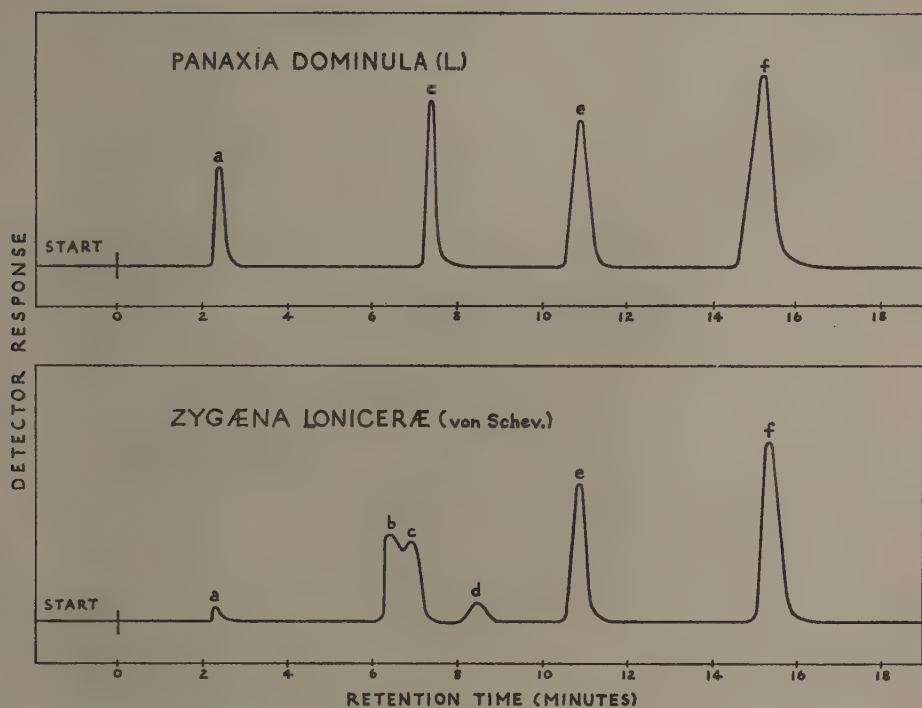


FIG. 7.—Chromatograms of the Scarlet Tiger (*Panaxia dominula* (L.)) and 5-spot Burnet (*Zygæna lonicerae* (von Schev.)). Collection from whole insect.
Column: Apiezon "L". Temperature: 66° C.

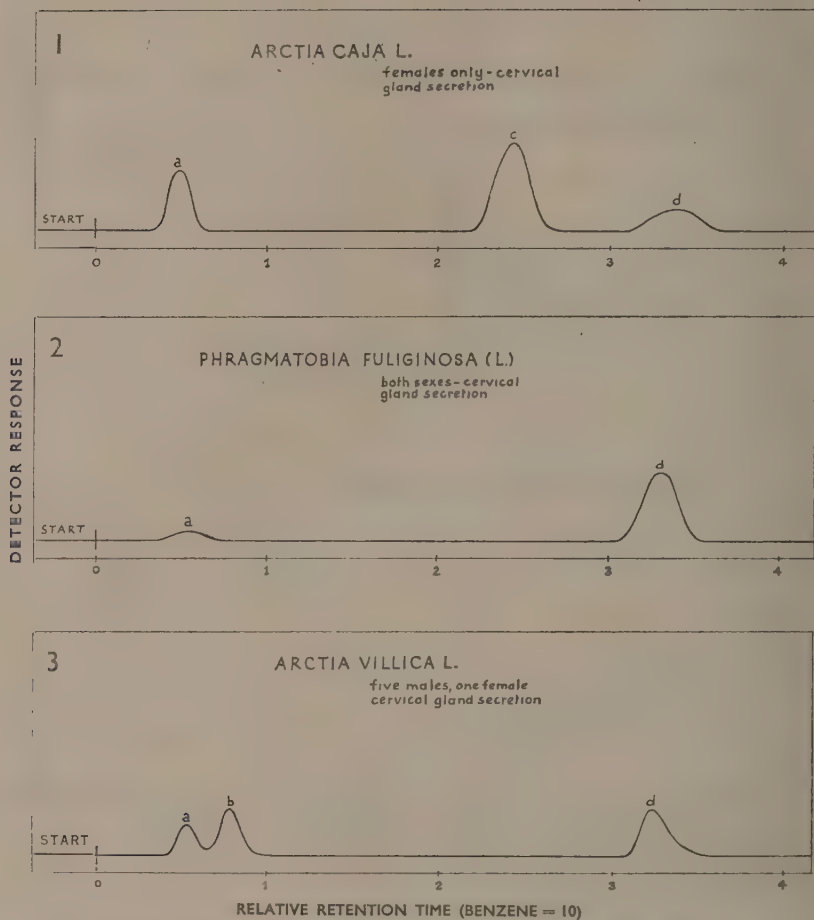


FIG. 8.—Chromatograms of secretion from cervical gland of Garden Tiger (*Arctia caja* L.), Ruby Tiger (*Phragmatobia fuliginosa* (L.)), Cream-spot Tiger (*Arctia villica* L.).
 Column: Dinonyl phthalate. Temperature: 20° C.

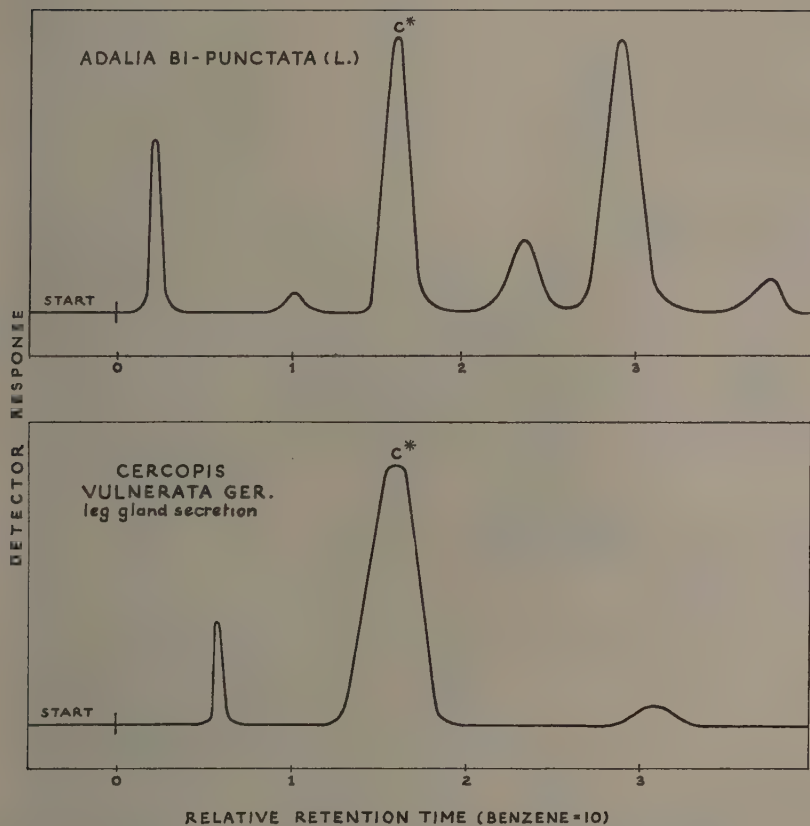


FIG. 9.—Chromatograms comparing the leg-gland secretion of the 2-spot Ladybird (*Adalia bi-punctata*) and the Froghopper (*Cercopis vulnerata* Ger.).
Column: Dinonyl phthalate. Temperature: 20° C.

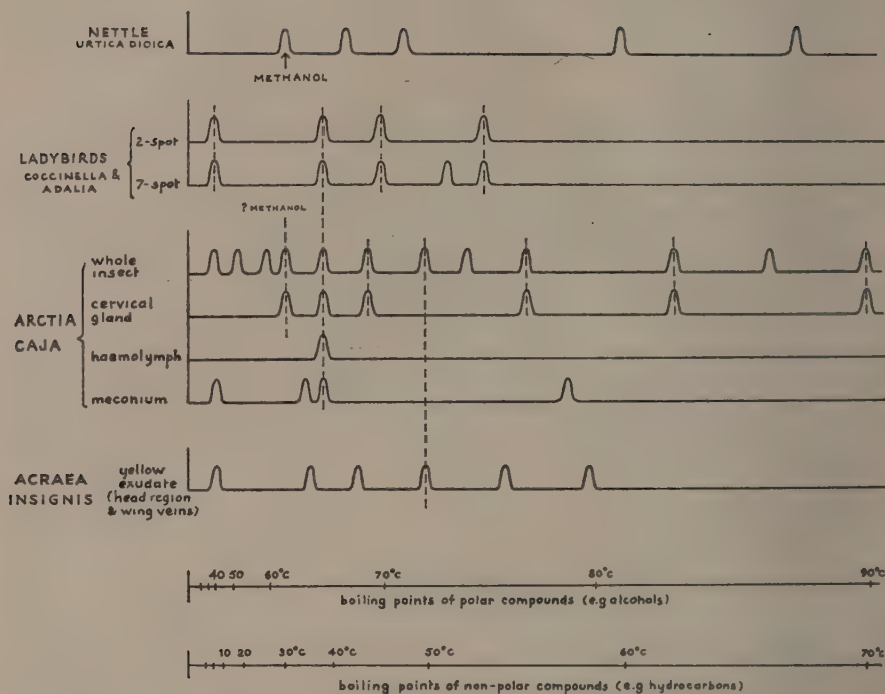


FIG. 10.—Schematic diagram of the chromatograms obtained for various species (Silicone oil column at room temperature).

Dotted lines are drawn through peaks indicating similar substances.

APPARATUS FOR COLLECTING VOLATILE MATERIAL FROM MOTHS

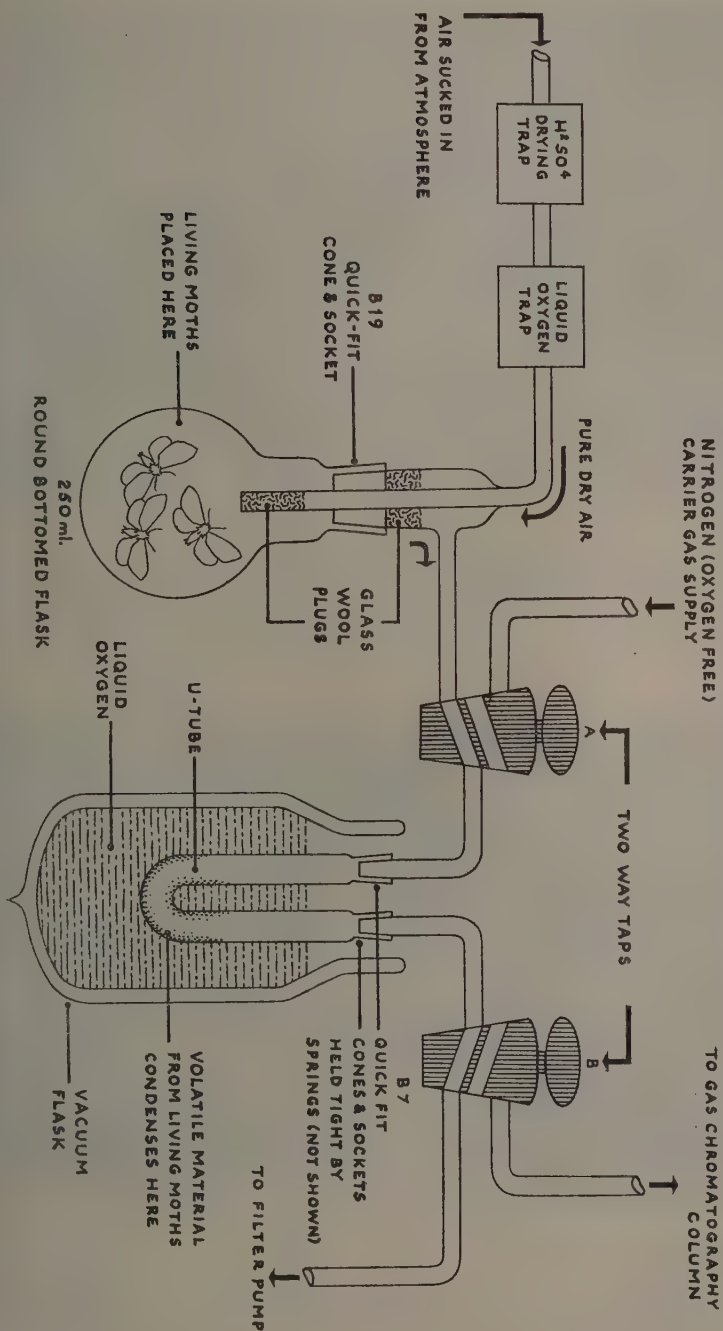


FIG. 11.—Diagram of apparatus for collecting volatile material from moths. Vapour can be collected from the flask containing living moths or from impregnated filter paper introduced directly into the U-tube.



FIG. 1.—*Arctia caja* (L.) displaying. The antennae are poked forward, the red hind wings fully exposed, and the patagia raised, thereby exposing the fringe of red hair and the site of the defensive cervical glands. Two colourless drops of secretion can be seen oozing from the dorsal apertures of these glands. It is at this early stage that the smell from the defensive fluid is most powerful. Later the fluid turns yellow when haemolymph mixes with the initial secretion.



FIG. 2.—*Panaxia dominula* (L.) displaying. This type of display takes a more passive form. Although the red hind wings are exposed the antennae, legs, etc. become flaccid and the whole moth limp and motionless. Neither *A. caja* or *P. dominula* will fly if poked or irritated during this stage of the display, the one becoming more rigid the other more flaccid, but both remain motionless. In the case of *P. dominula* haemolymph appears to be pumped out immediately through the gland apertures of the defensive glands, together with the powerful, evil smelling secretion. The flow is more copious than in the case of *A. caja* and a brighter yellow in colour. In the above photograph drops of the secretion can be seen near the base of the antennae. Note the two yellow warning marks on the prothorax which simulate drops of defensive fluid.



FIG. 3.—*Spilosoma lubricipeda* (L.) feigning death. No active display was observed in this moth but if handled or tapped in a certain manner it “feigns death” and drops on to the ground. Lying on its back the yellow parts of the body are much in evidence and the legs are held in a position which fully exposes their yellow hairs. The apertures of the defensive glands are much more ventral in this species and thus the drops of defensive secretion when expressed are more obvious and effective when the insect is lying on its back. In the above photograph a drop of this secretion can be seen at the base of the antennae.

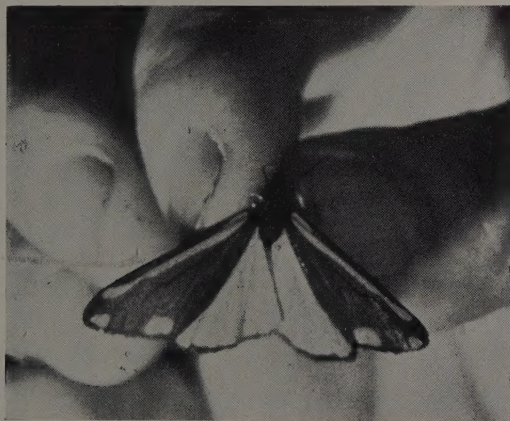


FIG. 4.—*Hypocrita jacobaeae* (L.) nipped between finger and thumb. The secretion from the defensive glands of this moth is also expressed when the moth is handled. Freshly emerged moths in the wild are said to be able to squirt the fluid from these glands for a distance of several centimetres (Windecker, 1939), but this has not been observed in British material. Since a special stimulus is often required to release a particular defensive response, some part of a display may be entirely overlooked. The blood-cell count in the defensive fluid of *H. jacobaeae* is relatively very high.

